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MADRÑO

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PINUS OAXACANA, A NEW SPECIES FROM MEXICO

N. T. MIROV

In Oaxaca and adjacent states of Mexico is found a pine with very long, prominent projections of the apophyses of the cone scales. Though previously identified as a variety of *Pinus pseudostrobus* Lindl., this pine differs from *P. pseudostrobus* especially in the cones and in the chemical composition of the turpentine, and it is here published as a new species.¹

Pinus oaxacana Mirov, sp. nov. *P. pseudostrobus* var. *apulcensis* Shaw pro parte, as to two specimens cited, not as to type, Pines of Mexico, p. 19, 1909. Non *P. apulcensis* Lindley, Edwards' Bot. Reg. 25, Misc. 63, 1839. *P. pseudostrobus* var. *oaxacana* Martínez as to description, not as to type, Las Pinaceas Mexicanas 1:195. 1945. Oaxaca pine. *Pinus* subgenus *Diploxylon* Koehne. Arbor 20–30 m. alta, ramulis vernis uninodalibus, glaucis; folia 5 in fasciculo, 20–33 cm. longa, serrulata, tenuissima, flexilia, pendula; stomata dorsalia pleurumque 5–7 seriebus et stomata ventralia 3–5 seriebus untrinque; hypodermis 2–4 seriebus cellularum, uniformis vel multiformis; ducti resinosi mediani, 2–4; endodermis cum septis exterioribus cellularum crassis; fasciculi vasculares 2, approximati; vaginae ca. 28–18 mm. longae, persistentes; strobili subterminales, 1–3, subsessiles, 10–14 cm. longi, clausi ca. 6 cm. lati, aperti ca. 9–11 cm. lati, ovoidei vel conici, acuti, leviter asymmetricales vel obliqui, ad maturationem aperientes, decidui super squamas infimas; apophyses ca. 12–20 mm. latae et ca. 8–12 mm. altae, rhomboideae, crassae, carinatae, cum projectione prominenti elongata 5–22 mm. longa, basi 5–12 mm. lata et 3–8 mm. crassa, pyramidalis vel conica, durā, complanata, recta vel curvata et reflexa; umbo in parte exteriori projectionis in puncto brevi terminens; projectiones inaequales, ad latum abaxialem strobili longiores; semen 6–7 mm. longum, obovoideum, atro-brunneum, cum ala separabili brunnea ca. 20 mm. longa et 8–9 mm. lata.

Resina terebintha n-heptane, 21 per centum; dextro- et dextro, laevo- α -pinene, 51 per centum; laevo- et dextro, laevo-limonene, 15–16 per centum; n-undecane, 1.3 per centum; et sesquiterpene, longifolene, 7.5 per centum componitur.

Tree 20–30 m. tall, the spring shoots uninodal, glaucous; leaves 5 in a fascicle, 20–33 cm. long, serrulate, very slender, flexible, drooping; dorsal stomata mostly 5–7 rows and ventral stomata 3–5 rows on each side; hypodermis of 2–4 layers of cells, uniform or multiform; resin ducts medial, 2–4; endodermis with outer cell walls thick; vascular bundles 2, close together; sheaths about 28–18 mm. long, persistent; cones subterminal, 1–3, subsessile, 10–14 cm. long, ovoid or conic, acute, slightly asymmetrical or oblique, opening at maturity, deciduous above lowest scales; scales

¹ Dr. Elbert L. Little, Jr., of the United States Forest Service, assisted in preparing the Latin and English descriptions and in checking the nomenclature.

with apophyses ca. 12–20 mm. broad and 8–12 mm. high, rhomboidal, thick, keeled, the apophyses with projections prominent, elongate, unequal (those on abaxial side of cone longer), 5–22 mm. long, 5–12 mm. wide at base, 3–8 mm. thick at base, pyramidal to conic, hard, flattened, straight or curved and reflexed, the umbo on outer part of each projection ending in a short point; seeds 6–7 mm. long, obovoid, dark brown, with detachable brown wing ca. 20 mm. long and 8–9 mm. wide.

The turpentine is composed of n-heptane, 21 percent; d, dl- α -pinene, 51 percent; l, dl-limonene, 15–16 percent; n-undecane, 1.3 percent; and a sesquiterpene, longifolene, 7.5 percent.² A herbarium specimen which serves as a voucher for the turpented trees was collected near Rancho Nuevo, 65 kilometers southwest of San Cristobal de Las Casas, Chiapas, Mexico (Mirov, in 1951) and is deposited at the Institute of Forest Genetics, Placerville, California.

Holotype. Near La Parada, Oaxaca, Mexico, altitude 7,500–9,000 feet, August 18, 1894, *E. W. Nelson 985* (US 398558). A slightly reduced drawing of the cone of the holotype which is about 13 cm. long, was reproduced by Shaw (1909, pl. 12, fig. 8; 1914; pl. 24, fig. 214). Another cone illustrated by Shaw (1909) is: *E. W. Nelson 2539* (US 398583), Miahuatlán, Oaxaca.

Under the name *P. pseudostrobus* var. *oaxacana* Martínez, detailed descriptions and good illustrations of *P. oxacana* were published by Martínez (1945, pp. 195–201; 1948, pp. 202–9) and by Loock (1951, pp. 161–164). In addition, both of these writers recorded it as occurring in the states of Oaxaca, Mexico, Puebla, Guerrero, Veracruz, and Chiapas.

In his treatment of the pines of Mexico, Shaw (1909) included this taxon as a variety of *P. pseudostrobus* Lindley (Edwards' Bot. Reg. 25, Misc. 63, 1839), basing his concept on Lindley's *P. apulcensis* (ibid.) and characterizing it as having "a greater or less prolongation of the apophyses." Shaw cited and illustrated three specimens: *E. W. Nelson 985*, La Parada, Oaxaca; *E. W. Nelson 2539*, Miahuatlán, Oaxaca; and *Pringle 8788*, Eslava, Distrito Federal. He assumed that all these specimens, as well as a cone collected by Hahn in 1866 at Cofre de Perote, Veracruz, and in the Museum d'Histoire Naturelle in Paris, were the same as *P. apulcensis* Lindl. from Apulco, Hidalgo.

Martínez (1945, pp. 168–201; 1948, pp. 184–209) recognized within *P. pseudostrobus* six variations (the typical variety, four named varieties and one form), differing chiefly in cone scale characters. Two of these named varieties and the form are pertinent herein. He showed clearly that the two Nelson Oaxaca collections, cited by Shaw as *P. pseudostrobus* var. *apulcensis*, belong to another taxon which he (Martínez) illustrated and described (in Spanish, loc. cit.) as *P. pseudostrobus* var. *oaxacana*. Unfortunately, Martínez failed to cite a type specimen, to publish a Latin

² This information was obtained from one sample, in which oleoresin from 25 trees was combined. In other samples the percentages may be different. Of significance is the presence of large quantities of a paraffin hydrocarbon, normal heptane.

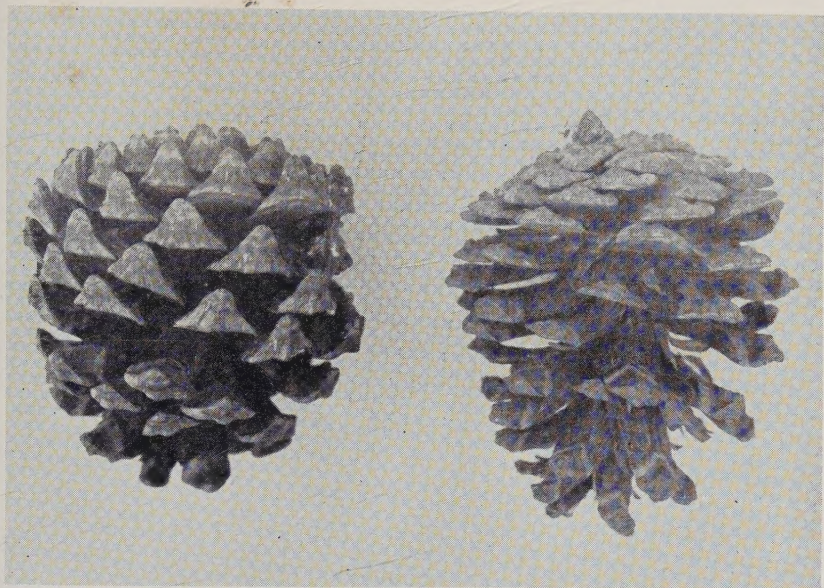


FIG. 1. Cone of *P. pseudostrobus* (left) ; cone of *P. oaxacana* (right). Both ca. $\times \frac{1}{3}$. Photo courtesy California Forest and Range Experiment Station, U. S. Forest Service.

diagnosis, or to designate the synonym *P. pseudostrobus* var. *apulcensis* (Lindl.) Shaw as applicable to his material only "in part." Therefore, although his intent was clearly otherwise, the name *P. pseudostrobus* var. *oaxacana* of Martínez must be referred to the type specimen (Hartweg in 1838, Apulco, Hidalgo) upon which both *P. apulcensis* Lindl. and *P. pseudostrobus* var. *apulcensis* (Lindl.) Shaw are based. Hence, it has been necessary to present a formal description and typification of the taxon represented by the Nelson Oaxaca specimens. To the pine from Apulco (*P. apulcensis* Lindley), Martínez (1945, p. 192; 1948, p. 199) assigned the name *P. pseudostrobus* var. *apulcensis*, an epithet which was superfluous when published, inasmuch as Shaw had already published this combination in 1909.

Under *P. pseudostrobus* var. *apulcensis*, Shaw cited a third collection with least prominent apophysis, *Pringle 8788* from Eslava, Distrito Federal. This collection had been distributed as *P. pseudostrobus* but had the synonym *P. protuberans* Roehl also on the printed label. *Pringle 8788* is therefore referred to *P. pseudostrobus* forma *protuberans* Martínez (1945, p. 184; 1948, p. 192), which was characterized by the protuberant apophysis ending in a sharp point and which was recorded from Eslava as well as other localities.

However, it becomes desirable to establish the identity of the century-old prior species *P. protuberans* Roehl (Cat. Grain. Conif. Mex. 27, 1857) from 9,000–10,000 feet altitude near Contreras, Distrito Federal. Bene-

dict Roezl (1824–85), a Czech plant collector and horticulturist, in 1857 and 1858 published names of nearly one hundred new species of *Pinus*, mostly from the vicinity of Mexico City, in two commercial catalogs of Mexican conifers. The original descriptions of Roezl's species were republished and translated by other authors, of which the following may be cited for *P. protuberans*: German, condensed, by Otto (Hamburg. Gart. Blumenzeit. 13:408. 1857); English by Gordon and Glendinning (Pinetum 259. 1858); Latin by Schlechtendal (Linnaea 29:348. 1858); and the original French by Carrière (Traité Gén. Conif. Ed. 2, 522. 1867).

Actually, Roezl characterized the five members of his Section VIII of *Pinus* as having five long needles and very prominent apophyses and protuberances, characters which indicate close relationship with the *P. pseudostrobus* complex and with *P. oaxacana*. Besides *P. protuberans*, this section had three other new species, *P. angulata* Roezl, *P. exserta* Roezl, and *P. heteromorpha* Roezl, and also *P. rudis* Endl. (a misapplication of that name).

Gordon (Sup. Gord. Pinetum 70, 1862; Pinetum Ed. 2, 319, 1875) examined Roezl's specimens and accepted *P. protuberans* Roezl, giving the other species of Roezl's Sect. VIII as synonyms under *P. protuberans*. Carrière (*ibid.*) also accepted *P. protuberans* Roezl, quoted the original description, and published a longer description of Roezl's dry specimens and living young plants. He reduced two species to varieties [*P. protuberans angulata* and *P. protuberans exserta*], and retained *P. heteromorpha* Roezl as a species. Parlatores [in DC., Prodr. 16(2):401–402. 1868] reduced *P. protuberans* and *P. heteromorpha* to synonymy under *P. pseudostrobus* Lindl. and placed *P. angulata* and *P. exserta* under *P. montezumae* Lamb. In a summary of 82 new species of *Pinus* in Roezl's catalog of 1857, Shaw (1909, p. 3 and table) cited the above and other references, noted that many of Roezl's specimens had been lost, and concluded that there was not a single valid species among the six or seven pines represented.

The epithets *P. protuberans* Roezl and *P. pseudostrobus* forma *protuberans* apparently refer to the same entity. The cone scale of *P. protuberans* has a protuberance, while that of *P. oaxacana* has a longer, more prominent projection. Therefore, because of the morphological and geographical differences, this pine from Oaxaca is not referable to any of Roezl's species.

Pinus oaxacana differs from typical *P. pseudostrobus* by the prominent projections of the apophyses of the cone scales. In the general part of his Los Pinos Mexicanos (Martínez, 1948, p. 37), Martínez showed drawings of the cone scales of his variety *oaxacana* and of *P. coulteri* D. Don as examples of protuberant apophyses.

When I collected oleoresin of Oaxaca pine in 1951 in Chiapas, Mexico, I found typical *P. pseudostrobus* and *P. oaxacana* growing together and I was much impressed by the difference in the cones. The heavy cones of Oaxaca pine resembled the cones of Shaw's group *Macrocarpae* (1914) more than the cones of typical *P. pseudostrobus*.

Shaw's group *Macrocarpae* consists of *Pinus torreyana* Parry, *P. coulteri* D. Don and *P. sabiniana* Dougl. In my opinion *P. jeffreyi* Murr. also is closely related to this group since, among other considerations, it crosses naturally with *P. coulteri*. Besides the morphological and genetic affinities of these pines, they all have common biochemical characters. Their turpentines all contain aliphatic hydrocarbons, either normal heptane C_7H_{16} or normal undecane $C_{11}H_{24}$ or both (Table 1).

Turpentine of *Pinus pseudostrobus* was analyzed by Iriarte (1946), and was found to contain over 90 percent of d- α -pinene and a small quantity of an unidentified sesquiterpene. Turpentine of *P. oaxacana* has an entirely different composition. It contains: n-heptane, 21 percent; d, dl- α -pinene, 51 percent; l, dl-limonene, 15-16 percent; n-undecane, 1.3 percent; and a sesquiterpene, longifolene, 7.5 percent (Iloff and Mirov, 1953). Chemically *P. oaxacana* has much more in common with the pines of the group *Macrocarpae*, including *P. jeffreyi*, than with *P. pseudostrobus* (Table 1).

TABLE 1. OCCURRENCE OF SOME CHEMICAL SUBSTANCES IN THE TURPENTINES OF SEVERAL PINES

	n-heptane	α -pinene	limonene	n-undecane	longifolene	aldehydes	β -phellandrene
<i>P. jeffreyi</i>	+	+	+
<i>P. sabiniana</i>	+	+
<i>P. coulteri</i>	+	+	+	+	+
<i>P. torreyana</i>	+	+	+	+	+
<i>P. oaxacana</i>	+	+	+	+	+
<i>P. pseudostrobus</i>	+	?

The proposal to elevate Oaxaca pine to a specific rank is based on consideration of both morphological and biochemical characteristics of the pine. The use of biochemical characters for taxonomic purposes is gaining more and more ground among taxonomists, especially in view of the brilliant research on Australian trees by Penfold (1935) and his co-workers. Among the pines, *Pinus jeffreyi* is an outstanding example of the validity of biochemical characters in taxonomy. This pine has been considered by some botanists for a long time as a variety of *P. ponderosa* (Shaw, 1914). Lately, however (and at least, partly because of profound chemical differences of the two pines) *P. jeffreyi* has been reinstated to its original status as a valid species.

Pinus oaxacana apparently crosses naturally with *P. pseudostrobus*. It is entirely possible that great variability in the structure of the cone scales within the *P. pseudostrobus* complex has been caused by hybridization

between these two pines. *Pinus oaxacana* also probably crosses with some varieties of *P. montezumae*, but consideration of such behavior is beyond the scope of this paper.

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CHROMOSOME COUNTS IN SECTION ERYTHRANTHE OF THE GENUS MIMULUS (SCROPHULARIACEAE)¹

ROBERT K. VICKERY, JR., BARID B. MUKHERJEE, AND DELBERT WIENS

Brozek (1932) of Charles University, Prague, has determined the chromosome numbers of three horticultural plants of *Mimulus cardinalis* to be $2n = 16$. These counts were made in connection with his investigation of the genetics of flower color in this species. The senior author also has carried on work on the inheritance of flower color in the *M. cardinalis* complex (Vickery and Olson, 1956). In addition he is undertaking a bio-systematic study of the group. These investigations have necessitated a survey of the chromosome numbers of both the horticultural populations and the cultures of the wild races being used in these two studies. Herbarium specimens of all the cultures counted are deposited in the Garrett Herbarium of the University of Utah under the culture numbers given in Table 1.

¹ The work was supported by grants from the National Science Foundation and the University of Utah Research Fund. The authors wish to thank Drs. W. W. Newby and C. M. Woolf for their helpful criticisms of the manuscript.

TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION ERYTHRANTHE

A. CULTURES OF NATIVE SPECIES

- n = 8 *M. lewisii* Pursh
 Porcupine Flat, Mariposa County, California, altitude 8000 feet,
 Sept. 17, 1948, *Hiesey* (5032).
 Above Alta, Salt Lake County, Utah, altitude 8700 feet, *Vickery* 207
 (5875).
- n = 8 *M. verbenaceous* Greene
 Narrows Trail, Zion National Park, Washington County, Utah,
 altitude 4400 feet, April, 1956, *Wiens* (5264).
 Bright Angel Creek, near Phantom Ranch, Grand Canyon National
 Park, Coconino County, Arizona, altitude 2000 feet, Nov. 4, 1954,
Jackson (5924).
- n = 8 *M. cardinalis* Dougl.
 Beaver Creek, Siskiyou County, California, altitude 1800 feet,
Hiesey 555 (5031).

B. CULTIVATED COLOR FORMS

- n = 8 *M. cardinalis* Dougl.
- 5077 Royal Botanic Garden, Edinburgh, Scotland.
 - 5078 Regional Park Botanic Garden, Berkeley, California.
 - 5308 Botanic Garden, Halle, Germany.
 - 5309 Botanic Garden, Basel, Switzerland.
 - 5310 Botanic Garden, St. Gallen, Switzerland.
 - 5311 University Botanic Garden, Liège, Belgium.
 - 5312 Botanic Garden, Antwerp, Belgium.
 - 5313 Botanic Garden, Wageningen, Netherlands.
 - 5315 University Botanic Garden, Brno, Czechoslovakia.
 - 5316 Botanic Garden, Cluj, Roumania.
 - 5318 Botanic Garden, Copenhagen, Denmark.

Brozek made his counts from the tips of adventitious roots, fixing them in Navashin's fluid and staining them with either Heidenhain's iron haematoxylin or Cajal's magenta and picro-indio-carmine stain (Brozek, 1932). We obtained good results with the method previously described (Mukherjee, Wiens, and Vickery, 1957) which employs fixation of the buds in acetic or propionic acid followed by squashing and staining in either aceto-carmine or propio-carmine.

The sources of the horticultural color forms and of the wild cultures which we have studied are given in Table 1. The chromosome number appears to be $n = 8$ in all cases (fig. 1) although the preparations of *M. verbenaceous* (5264) showed occasional cells with apparently 9 or 10 chromosomes instead of the usual 8. The chromosomes of the 5077 culture of *M. cardinalis* were noticeably larger than the average for other races of the species (fig. 1). Those of the 5875 culture of *M. lewisii* were appreciably smaller than those of any other culture of the complex which we have examined. These size differences in the chromosomes suggest that there may be structural differences which in turn may account for the barriers to hybridization which we have observed when crossing *M. cardinalis* and *M. lewisii* (Vickery, 1956). Initially, all crosses produce vigorous F_1

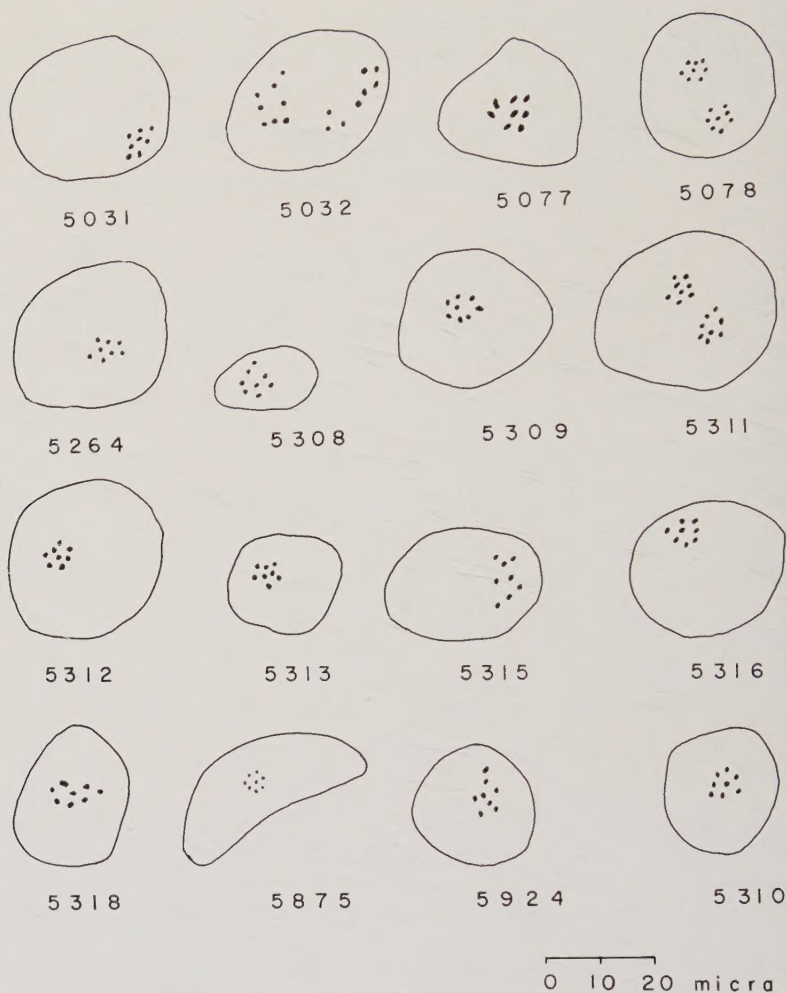


FIG. 1. Meiotic chromosomes of pollen mother cells of *Mimulus*, $\times 750$. Chromosome numbers of all the cultures are $n = 8$. Camera lucida drawings were made in all cases. The pollen mother cells of cultures 5077, 5264, 5308, 5309, 5318, and 5875 are in first metaphase whereas all the others are in second metaphase, but the two figures of the second metaphase were drawn only if the counts were clear in both nuclei.

populations but frequently the F_2 and F_3 generations are marked by decreased fertility. The crosses between *M. verbenaceous* and *M. cardinalis* and between *M. verbenaceous* and *M. lewisii* yield vigorous, fertile F_1 hybrids, also.

Combinations of *M. cardinalis* or *M. lewisii* with species of section *Paradanthus* consistently failed (Vickery, 1956). *Mimulus moschatus*

Doug., *M. primuloides* Benth., and *M. bioletti* Eastw. were used to represent section *Paradanthus*. Six different reciprocal crosses were attempted using an average of five flowers each. A *Paradanthus* intrasectional combination of *M. moschatus* and *M. floribundus* Dougl. produced vigorous but sterile F_1 hybrids. We have obtained only one chromosome count for this section: *M. moschatus*, $n = 16$ (unpublished).

On the basis of these genetic and cytological results we believe that the most natural taxonomic treatment is to group the three taxa, *M. cardinalis*, *M. verbenaceous*, and *M. lewisii*, in section *Erythranthe*. This treatment follows that of Pennell (1951) rather than that of Grant (1924) where *M. lewisii* is placed in section *Paradanthus*.

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TWO NEW SPECIES OF PENSTEMON IN COLORADO

C. WILLIAM T. PENLAND

Since the treatment of *Penstemon* for Harrington's "Manual of the Plants of Colorado" was prepared, additional collections and study have made it necessary to recognize the following two new species for the state.

Penstemon harringtonii sp. nov. Herba perennis, glabra, 3- dm. 7 alta; caulibus erectis, simplicibus, glaucis; foliis glaucis, integris, crassis, obtusis vel acutis, mucronatis, basalibus spathulatis vel oblanceolatis, 5-7 cm. longis, 1.5-2.5 cm. latis, caulinis ceteris parvioribus, sessilibus, obovatis, elliptico-ovatis vel cordato-amplexicaulibus, ad inflorescentiam versus gradatim reductis; thyrsos cylindraco, angusto, interrupto, 5-10-fasciculato; calyce 5-9 mm. longo, lobis ovato-lanceolatis, acutis vel acuminatis, scarioso-marginatis; corolla 18-24 mm. longa, coerulea (vel rosea), bilabiata, fauce ampliata; staminibus didynamis, inferioribus

corollae faucem multo excedentibus; antheris 2.5–3 mm. longis, glabris, sagittatis; loculis antherarum de apice ad basim dehiscentibus, confluentibus, haud explanatis; filamentum sterili dilatato (usque ad 1–1.5 mm. latitudine), pilis 1–2 mm. longis, dense aurato-barbato; capsulis ignotis.¹

Glabrous perennial, 3–7 dm. tall; stems one to few, simple, erect, glaucous below, often purplish, especially above; leaves entire, thickish, glaucous, mucronate, the basal 1.5–2.5 cm. wide, 5–7 cm. long, spatulate to oblanceolate, obtuse to acute, the lower cauline 1–2 cm. wide, 2–5 cm. long, obovate, elliptic or ovate, acute, the upper cauline gradually reduced, ovate to cordate-clasping; inflorescence cylindrical, of 5–10 rather lax-flowered fascicles, one-third to one-half or more the height of stem; peduncles surpassing bracts, especially above; bracts all acute, scarious-margined, the lower broadly sessile-clasping, the upper reduced and inconspicuous, longer than wide; calyx 5–9 mm. long, the lobes ovate- to lance-acuminate, striate, narrowly scarious-margined; corolla 18–24 mm. long, pale to deep coerulean blue, often lilac-tinged on tube, or strongly pinkish-lilac throughout, the throat ampliate-funnelform, rather distinctly bilabiate, the lower lobes divergent but scarcely reflexed, the upper arched-erect; stamens conspicuously didynamous, the upper pair attached to corolla at its very base, the lower pair attached along corolla tube for about one-half their lengths, the free part then curved ventrally in the throat and well-exserted outward and upward to bring anthers opposite middle of orifice of corolla; anthers 2.5–3 mm. long, glabrous, sagittate, attached to filament at their middle or below, the connective wide, the sacs conjoined for one-half or more of their lengths, dehiscing throughout but not explanate, remaining parallel but curved; staminode glabrous to middle, then abruptly densely bearded with golden yellow hairs, those on the upper surface 1–2 mm. long, those on the lower surface prominent, but shorter and less dense, the staminode widened distally to 1–1.5 mm., rounded at tip and curved ventrally, usually a little exserted from orifice of corolla tube; mature capsules not seen.

Type. Abundant in sagebrush, altitude about 8000 feet, 3–5 miles northwest of Green Mountain Dam, Grand County, Colorado, 19 June 1952, *Penland 4296* (COCO; isotypes, COLO, CS, GH, NY, RM, UC, US).

Other known collections. COLORADO. Eagle County: rather dry slope 5 miles east of Wolcott, elevation 7200 feet, 7 June 1951, *H. D. Harrington 4935* (COCO, CS). Routt County: pinyon, cedar, sage association, elevation 7500 feet, 2 miles north of McCoy, Highway 131, 29 June 1951, *M. & C. Norton s.n.* (COCO, CS).

Penstemon harringtonii is readily recognized both in the field and in the herbarium by its two well-exserted stamens (fig. 1), a character that appears remarkably constant. Judged on the basis of its anthers it is most closely related to *P. cyathophorus* Rydberg, and it is therefore referred to the section *Coerulei* (as defined by Pennell, 1935). It differs

¹ The assistance of Mr. Robert M. Ormes in preparation of Latin diagnoses is gratefully acknowledged.



FIG. 1. *Penstemon harringtonii*. Habit, ca. $\times \frac{1}{3}$; anthers, $\times 5$; staminode, ca. $\times 1\frac{1}{2}$; flower, $\times 1$.

from *P. cyathophorus* in its larger flowers (18–24 mm. long as compared to 9–15 mm.), in having only two instead of its four stamens strikingly exserted, in its longer anthers (2.5–3 mm. as compared with 2 mm.), and in its strongly reduced bracts, which are mostly longer than broad (the reverse is true of *P. cyathophorus*). In general appearance, however, *P. harringtonii* is more like *P. osterhoutii* Pennell (same section), to which it

was first referred, than it is like *P. cyathophorus*. Although the flowers average 14–20 mm. long in *P. osterhoutii*, thus approaching those of *P. harringtonii*, the anther sacs are widely divaricate and not at all sagittate as in *P. harringtonii*, and the stamens are not or scarcely exerted in *P. osterhoutii*. These closely related species may be keyed as follows:

Anthers sagittate with parallel sacs; 2 or all 4 stamens well-exserted.

Flowers 18–24 mm. long; only 2 stamens exerted; anthers 2.5–3 mm. long; bracts mostly longer than broad.....*P. harringtonii*

Flowers 9–15 mm. long; all 4 stamens exerted; anthers 2 mm. long; bracts mostly broader than long*P. cyathophorus*

Anthers with sacs divaricate; stamens not or scarcely exerted.....*P. osterhoutii*

The three cited collections of *P. harringtonii* represent a distribution of this plant on both sides of the Colorado River drainage system, and, to the south, on both sides of the Gore Range (Eagle and Blue rivers). The known range of *P. cyathophorus* (Grand and Jackson counties in Colorado, and in adjacent southern Wyoming) is to the north of that of *P. harringtonii* (Eagle, Grand, and Routt counties, Colorado), although at one place in Grand County the two species occur within 2–3 miles of each other. *Penstemon osterhoutii*, the other species closely related to *P. harringtonii*, is common to the west of *P. harringtonii* in Eagle and Garfield counties, but the ranges of the two do not overlap. Moreover, *P. harringtonii* occurs at elevations of 7200–8000 feet, while *P. osterhoutii* has not been collected above an elevation of 6600 feet.

The unusually interesting *Penstemon acaulis* Wms. was first collected in Sweetwater County of southwestern Wyoming. Later it was found in adjacent Daggett County in Utah. So far as is known it has not been reported from south of the Uinta Mountains in Utah, or from the northwestern corner of Colorado. In 1951 the writer collected a *Penstemon* which was at first presumed to be only a more robust form of *P. acaulis*. It was found a few miles east of Elk Springs, south of the Yampa River in Moffat County, Colorado, a locality approximately eighty airline miles southeast of the nearest known station for *P. acaulis*. In order to secure better diagnostic material this area was again visited in 1952 and 1953. In those years two additional stations for the plant were discovered; both of these were north of the Yampa River, between Greystone and the Little Snake River. The collections and all material observed in the field are quite uniform in aspect, and continued study has led to the proposal of the following new species, whose closest relative is clearly *P. acaulis*.

***Penstemon yampaensis* sp. nov.** Herba caespitosa perennis, 3 cm. vel minus alta; rhizomatibus ramosis; foliis 15–30 mm. longis, 2–4 (–5) mm. latis, oblanceolatis, acutis, cinereis, spiculato- vel papillato-pubescentibus, plus minusve viscidis; calyce 5–9 mm. longo, viscido-pubescente, lobis acuminatis, inferne scarioso-marginatis; floribus 2–4 in ramo terminali; corolla 15–18 mm. longa, pallide roseo-purpurea (vel demum coerulea), extus glanduloso-pubescente, basi faucis rotundatae haud pli-



FIG. 2. *Penstemon yampaensis* (Penland 4415). About $\times 1$.

catae aliquantulo ventricosae aureo-barbata, lobis posterioribus quam ceteris brevioribus; staminibus inclusis; loculis antherarum 1–1.5 mm. longis, glabris, confluentibus, haud late explanatis; filamentis sterilibus paulo exsertis, insuper aureo-barbatis; capsulis fere globosis, 4 mm. longis, glabris; seminibus 2–4, nigris, lunatis, rugosis.

Caespitose, essentially acaulescent perennial, spreading from branching rootstocks and in the open forming loose mats up to one foot in diameter, 3 cm. or less in height; leaves cineraceous, 15–25 (–30) mm. long, 2–4 (–5) mm. wide, oblanceolate, acute but not mucronate, scabro-pubescent with low, blunt, papilliform hairs (common on upper portion) or longer, straight or somewhat recurved, spiculate hairs (common toward base and petiole), the foliar hairs not gland-tipped but evidently viscid; mid-rib and two or more lateral veins prominent on dried specimens; flowers usually 4 (2–6) on each of the very short ultimate branches, often exceeded by the foliage; calyx 5–9 mm. long, the lobes long-acuminate, rather densely viscid-pubescent, narrowly scarious-margined below; corolla 15–18 mm. long, lilac, or with strong bluish tinge when older (?), on dried specimens usually blue, glandular-pubescent externally, golden- (to whitish-) bearded in throat below, the two upper lobes arched-erect, but little shorter than the less divergent three lower lobes (which may reach a length of 5 mm.), the throat moderately ampliate above short tube, some-

what ventricose, not at all plicate; stamens with longer pair reaching limb of corolla, the anther sacs 1–1.5 mm. long, ovate to oblong-ovate, glabrous, minutely denticulate along suture, divaricate, dehiscent confluent, not explanate; the staminode exerted from throat, bearded all along its dorsal surface with golden hairs, a little widened distally (to as much as 0.75 mm.), the apex emarginate; capsules nearly globose, about 4 mm. long, glabrous at maturity; seeds lunate, 2–3 mm. long, black, rugose and punctulate, 2–4 per capsule.

Type. Sandy, calcareous knoll, scattered grass and sage; 5.5–6 miles east of Elk Springs, Moffat County, Colorado, 9 June 1953, *Penland 4415* (COCO; isotypes, COLO, GH, NY, RM, UC, US). All other collections are from Moffat County, Colorado: type locality, 26 June 1951, *Penland 4236* (topotype, COCO); type locality, 20 June 1952, *Penland 4311* (topotypes, COCO, COLO, CS, GH, NY, RM, UC, US); 20 miles south of Vermillion Creek Bridge, 22 June 1952, *Penland 4326* (COCO, UC, US); 3–4 miles south of Greystone, 10 June 1953, *Penland 4426* (COCO, NY, RM).

A key serving to separate *P. acaulis* (fig. 3) and *P. yampaensis* (fig. 2) follows:

Leaves essentially linear, 1–1.5 mm. wide, 10–20 mm. long; flowers 1 (–2) per ultimate floriferous shoot; corolla 14–16 mm. long, blue.....	<i>P. acaulis</i>
Leaves oblanceolate, 2–4 (–5) mm. wide, 15–25 (–30) mm. long; flowers usually 4 (–6) per ultimate floriferous shoot; corolla 15–18 mm. long, lilac to bluish-lilac	<i>P. yampaensis</i>

The foliar pubescence of these two species is essentially the same, though more of the spiculate hairs seem to be present in *P. yampaensis*, especially toward the leaf base. *Penstemon acaulis* was assigned to the section *Caespitosi* by Williams in his original description of this species (1934). Keck (1937) also assigned it to this group but changed the rank of the group to a subsection of the section *Ericopsis*. Keck pointed out, however, that in *P. acaulis*, "The character of its pubescence is unique in this group of species." There are two probable reasons for this uniqueness: 1) the papillate hairs, besides being short and blunt, are very broad at the base (commonly 44–73 microns, as compared to 14–25 microns for hairs of *P. caespitosus* Nutt., *P. crandallii* A. Nels., *P. retrorsus* Payson and *P. abietinus* Pennell, all of which Keck also places in the *Caespitosi*; 2) the external walls of these hairs in *P. acaulis* and *P. yampaensis* are smooth or nearly so, while those of the four species named just above are denticulate (as observed in boiled or cleared material, at 100 × magnification). In this connection it is of interest that the hairs of *P. moffatii* Eastw. (section *Aurator*) are also blunt and smooth-walled. Also, the apex of some leaves of *P. moffatii* may even show the papillate condition of *P. acaulis*, but the longer, blunt, recurved type of hair is typical for the species.

The midrib of leaves of dried specimens of both *P. acaulis* and *P. yampaensis* is prominent nearly throughout; in addition, *P. yampaensis* shows



FIG. 3. *Penstemon acaulis* (Penland 4419). About $\times 1$.

two or more prominent lateral veins. This type of veining is certainly rare in the *Caespitosi*. Although the midrib may be prominent, as in *P. crandallii*, this condition is found only in the petiolar portion of the leaf. In fact, I have found a leaf situation similar to *P. yampaensis* in only one other case, a specimen from the Uinta Mountains of Utah which I have doubtfully referred to *P. abietinus*. Two other collections of *P. abietinus* show leaves agreeing with the other *Caespitosi*. (I have not studied leaves of *P. thompsoniae* (Gray) Rydb., however.) The midrib of *P. yampaensis* is not only prominent but is also relatively large (sometimes over 400 microns in diameter in cleared material, as compared with under 200 microns in *P. caespitosus*). Probably correlated with the presence of large lateral veins in *P. yampaensis* is the fact that a number of leaves have been found showing 1-4 small teeth near the apex.

The non-plicate character of the corolla throat certainly poses a question as to the assignment of *P. acaulis* and *P. yampaensis* to the subsection *Caespitosi*, where their caespitose nature would apparently place them. In all the other six species of the subsection (Keck, *loc. cit.*), the 2-ridged and commonly laterally flattened, plicate throat is a constant and diagnostic feature. Nor do *P. acaulis* and *P. yampaensis* fit into the other two subsections of *Ericopsis* (*viz.*, the *Linarioides* and the *Laricifolii*). It seems to me that their affinity is rather with the section *Aurator*, through such species as *P. nanus* Keck, *P. doliis* Jones, *P. pumilus* Nutt., and *P.*

moffatii Eastw. Perhaps the least that can be said for them is that they help to emphasize more strongly the relation between the sections *Aurator* and *Ericopsis*, a point which was elucidated by Keck.

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PECULIARITIES OF THE COLUMBIA RIVER GORGE FLORA

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The gorge cut through the Cascade Range by the Columbia River as it flows westward between Washington and Oregon has long been recognized as a place of peculiar botanical interest. If one studies the distribution of the plant species found there, he is soon impressed by the large number that are either endemic to the area or occur as isolated populations significantly removed from their normal range. My interest in the history of the various elements of the Pacific Northwest flora led me to speculate upon the meaning of these peculiar distributional patterns. It seemed possible that an analysis of them might furnish clues to the rôle the Columbia Gorge has played in the migrations of vegetation in the past. Its physiography and geographical relationship to adjacent vegetation areas would in themselves lead one to believe that it might have served as a pathway for the migration of many types of organisms. With this in mind, I have spent considerable time during the past few summers studying the local distribution of those plant species occurring within the Gorge. This field work has subsequently been supplemented with herbarium studies on their wider distribution. The present paper is the result of this work.

The species listed herein by no means constitute a complete flora of the Columbia Gorge, although I have tried to make the lists as inclusive as possible. The collections of other botanists who have collected extensively here have also been studied, particularly those of Howell, Gorman, Henderson, Suksdorf, and Sheldon. Nevertheless, further search would undoubtedly reveal more species which might be included in the roster. However, I am confident that the list is sufficiently extensive to give us a good general picture of the significant features of the Gorge flora as a whole, its distribution in the various habitats, and its relation to outside populations, which was the chief purpose of this investigation. Any additions to the number of species will not increase the accuracy of a study made from this particular viewpoint.

PHYSIOGRAPHY AND CLIMATE OF THE GORGE

The Cascade Range has been formed by a combination of gradual uplift since the Miocene epoch and of volcanic action largely during the Pliocene and Pleistocene. During this process the Columbia River, without materially altering its course, kept pace with the change by cutting its bed deeper and deeper, thus forming the great gash through the mountains which we know as the Columbia River Gap, or in a more restricted sense the Columbia River Gorge. Lateral erosion has been much slower than that carried on by the main stream, resulting in a deep canyon with precipitous walls, extending for some thirty-five miles. The small streams which flow into the river have cut their beds back into this canyon wall sometimes as much as a half mile, forming deep, narrow, lateral gorges into which the streams frequently plunge as waterfalls from a hundred to several hundred feet high.

Erosion has been less effective on the south wall of the canyon than on the north, and it is here that the most spectacular cliffs are to be seen. One of the most striking of these is the north face of St. Peter's Dome, which rises abruptly for about twenty-five hundred feet. Some of the cliffs have their bases almost at the river's edge, while others rise as much as a half mile or more back from the water. On the north wall of the Gorge the bases of the sheer drops are usually farther back from the river as well as higher up. A noticeable feature of both walls of the canyon is the frequent stair-step arrangement, apparently due to differences in hardness of the various strata of rock. It is of interest, but perhaps of no further consequence to us, that these steps, and therefore the shelves upon which much of the vegetation is growing, are roughly about six hundred feet one above the other. Thus there are a number of places where a shelf occurs about six hundred feet above the river, with other shelves above this at elevations of approximately twelve hundred and eighteen hundred feet. At most places the eighteen-hundred-foot shelf marks the top of the most abrupt cliffs, and the rise above that, while steep, is nevertheless a distinct slope, usually forested.

For an area so limited in extent the Columbia Gorge has an extremely varied climate. This is due in part to the depth of the canyon itself, in part to the influence of two entirely different climates at either end of the canyon, and in part to the general east-west orientation of the gap.

The curve of annual precipitation through the Gorge follows rather closely that of any transect extending from the Willamette Valley eastward across the Cascade Range to the central Oregon plateau. Although the level of the river bed rises comparatively little as one follows it eastward through the canyon, yet the elevation of the mountains that press in on either side is such as to raise the moisture-laden air masses from the Pacific Ocean sufficiently to cause a heavy precipitation over the central sector of the Gorge. The mean annual precipitation at Vancouver of 37 inches is typical for points along the lower Willamette and Columbia rivers. However, at Mount Pleasant, situated close to the western portal of

the Gorge, this figure has risen to 57 inches. Rainfall increases eastward to the vicinity of Cascade Locks where an average of approximately 75 inches is measured. Upstream from here there is a sharp drop in the annual mean. At Hood River and White Salmon about 30 inches are recorded, and at Lyle 25 inches.

Recorded data on temperatures in the Gorge do not tell us a great deal. Between Mount Pleasant and Hood River there is a gradual drop of 4.7°F . in the mean January temperature. In the same distance the mean July temperature rises 2.3°F .

One striking feature of the Gorge climate does not appear in the records. When atmospheric pressure differentials are favorable, masses of air move from eastern Oregon and Washington westward through the Gorge. In winter this situation frequently results in cold winds which at times reach very high velocities. When this occurs in conjunction with rainfall the result is often a very serious "silver thaw," i.e., a rain which freezes as it touches the ground, or trees and other vegetation. These freezing rains sometimes last for several days, and the breakage of trees and destruction of other types of plant life may be quite serious. A parallel situation frequently occurs during the summer when hot, dry east winds blow down through the gap, sometimes for several days at a time. The effect that such winds might have upon the vegetation is obvious.

As might be expected in a canyon with an east-west orientation, the local climate of the north wall is quite different from that of the south wall. This is clearly reflected in the difference in the general vegetation of the two sides. The flora of the dry, warm area of central Oregon and Washington extends much farther westward on the well-insolated south-facing slopes than on the north-facing wall, which is in deep shadow much of the time. On the other hand, the Douglas fir forest and its associates follow the cool north-facing slopes entirely through the Gorge to the Hood River Valley.

The significance of the Columbia Gap from the standpoint of such a climatic and vegetational barrier as the Cascade Range may be realized when we recall that it is the only point between the Fraser River in British Columbia and the Klamath River in northern California where the axis of the range has been cut through in such a way as to interrupt the continuity of all the life zones above the Transition. In this case the cutting has extended almost to sea level.

FLORA OF THE GORGE

To understand fully the flora of the Gorge and the implications of the distribution patterns of many of its species we must look first at the type of vegetation now existing in the adjacent lowlands at either end.

To the west the Gorge opens out upon what I have elsewhere called the Puget Area (Detling, 1948). This vegetation area occupies the broad valley between the Cascades and the Coast Range, extending from the south-

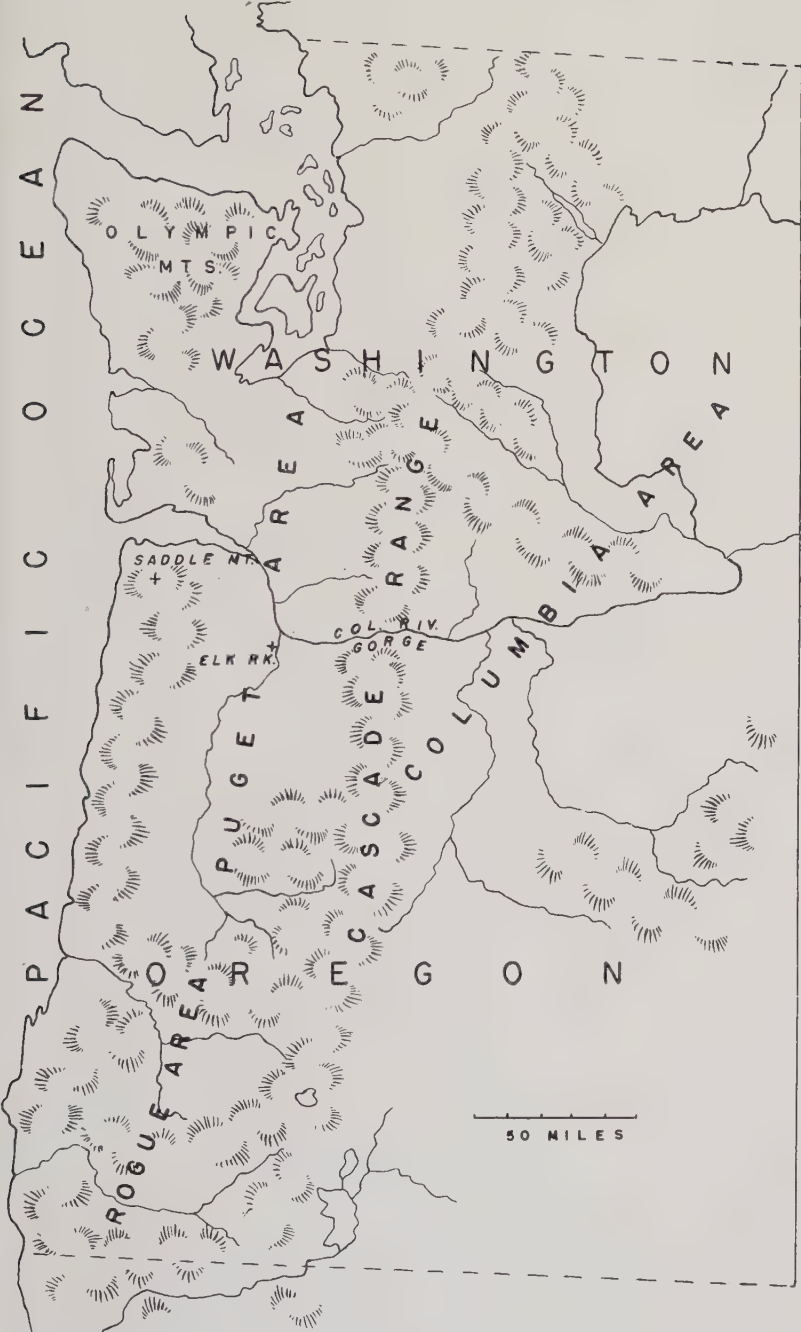


FIG. 1. Main geographic features of the Pacific Northwest related to the Columbia Gorge flora.

ern limits of the Willamette watershed in Oregon northward to Puget Sound and southern British Columbia. From a physiographic standpoint it coincides more or less with what the geomorphologists call the Puget Trough. The vegetation of the area is basically a Douglas fir forest, with an intermingling of oak-madrone woodland and grassland at lower levels and on the valley floor. Annual precipitation is high and neither summer nor winter temperatures are extreme. These conditions result in a dense forest cover, especially in the foothills, with an understory of vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), low Oregon grape (*Mahonia nervosa*), and red huckleberry (*Vaccinium parvifolium*), along with a wealth of herbaceous species.

Eastward the Gorge widens out and merges with the Columbia Area, again to use a name adopted by the author (op. cit.). This area occupies the valley of the Columbia River in north-central Oregon and south-central Washington, and such tributary valleys as those of the Yakima, John Day, and lower Deschutes rivers. The Hood River Valley comprises its westernmost extension. Annual precipitation is light throughout the area (13 inches at The Dalles). Winter temperatures are frequently very low, while the summers are hot. Apparently the region was originally a grassland, but there has been an invasion of sagebrush (*Artemisia* species) where the land has been overgrazed. Stands of ponderosa pine (*Pinus ponderosa*) are not uncommon on the hills where soil, moisture, and temperature conditions are favorable.

1. SPECIES OF WIDE DISTRIBUTION. For purposes of analysis I have found it convenient and useful to divide the Columbia Gorge species into groups according to their present general distribution. The first of these comprises a relatively large number of species (70, which is 34.0 per cent of the total of 206) which are widely distributed and occur at lower and middle elevations on both sides of the Cascade Range. From the standpoint of their origin this group can be divided again into two sub-groups—one whose members have probably come into our region from the north, the other evidently having originated to the south. In trying to determine where any given species has originated we may use several criteria. It is admitted that the use of any of these criteria alone would be unsound, but when they lend mutual support, and especially when applied to relatively recent migrations (from the standpoint of geological time), they probably present a fairly accurate idea of the direction of migration of most of the components of this flora. The criteria that seem most applicable to the problem at hand are: (a) The present maximum concentration of individuals of a species is likely to be somewhere near the area from which it has radiated in its migrations, and such concentration will probably be found in environmental conditions similar to those under which it originated. (b) A species is more likely to have come from a region where obviously close relatives are now located, than from a region in which such relatives are absent. (c) When a species typically occurs as a member of a definite species association, the area of origin of whose other

members can be postulated, we may assume it is safe to assign to it that same origin.

Judged on these bases the northern element of this first group consists of those species whose centers of distribution are to the north of the Columbia River; their present range frequently extends as far north as Alaska. At our latitude they are plants of shaded woodlands and stream banks, mostly associates of the coniferous forests. As might be expected from the dryness and high summer temperatures of the Columbia and Deschutes areas, the species tend to be absent from these two areas, but are common in the foothills and lower mountain slopes west of the Cascade crest and again in the Blue Mountains and in the Rocky Mountains of Idaho and Montana. It is highly probable that most of them migrated into our region by following the Cascade and Rocky Mountain ranges southward. The following species make up this sub-group:

<i>Adiantum pedatum</i> L.	<i>Mimulus guttatus</i> DC.
var. <i>aleuticum</i> Rupr.	<i>Physocarpus capitatus</i> (Pursh) Ktze.
<i>Aquilegia formosa</i> Fisch.	<i>Poa gracillima</i> Vasey
<i>Cerastium arvense</i> L.	<i>Poa nervosa</i> (Hook.) Vasey
<i>Chimaphila menziesii</i> (R.Br.) Spreng.	<i>Potentilla glandulosa</i> Lindl.
<i>Chimaphila umbellata</i> (L.) Nutt.	<i>Pseudotsuga menziesii</i> (Mirb.) Franco
var. <i>occidentalis</i> (Rydb.) Blake	<i>Pteridium aquilinum</i> (L.) Kuhn
<i>Circaea pacifica</i> Asch. & Mag.	var. <i>pubescens</i> Underw.
<i>Cirsium edule</i> Nutt.	<i>Rosa gymnocarpa</i> Nutt.
<i>Clintonia uniflora</i> (Schult.) Kunth.	<i>Rosa nutkana</i> Presl
<i>Cornus stolonifera</i> Michx.	<i>Rubus parviflorus</i> Nutt.
<i>Elymus glaucus</i> Buckl.	<i>Sambucus glauca</i> Nutt.
<i>Epilobium angustifolium</i> L.	<i>Sedum spathulifolium</i> Hook.
<i>Festuca occidentalis</i> Hook.	<i>Selaginella douglasii</i> (Hook. & Grev.)
<i>Festuca rubra</i> L.	Spring.
<i>Festuca subulata</i> Trin.	<i>Sisyrinchium idahoense</i> Bickn.
<i>Galium aparine</i> L.	<i>Smilacina racemosa</i> (L.) Desf.
<i>Geranium bicknellii</i> Britt.	<i>Smilacina sessilifolia</i> (Baker) Nutt.
<i>Heracleum lanatum</i> Michx.	<i>Symphoricarpos albus</i> (L.) Blake
<i>Heuchera micrantha</i> Dougl.	<i>Thalictrum occidentale</i> Gray
var. <i>pacifica</i> R.B.L.	<i>Thuja plicata</i> Donn.
<i>Linnaea borealis</i> L.	<i>Tiarella unifoliata</i> Hook.
var. <i>americana</i> (Forbes) Rehd.	<i>Trientalis latifolia</i> Hook.
<i>Lupinus polyphyllus</i> Lindl.	<i>Trillium ovatum</i> Pursh
<i>Lupinus rivularis</i> Dougl.	<i>Viola glabella</i> Nutt.
<i>Melica subulata</i> (Griseb.) Scribn.	

The species comprising the southern element of this first group have their present centers of distribution to the south of the Columbia River. None extends as far north as Alaska, although some reach southern British Columbia in the dry region east of the Cascades. West of the mountains they are most typically associated with the oak-madrone woodland, and when they occur at middle and higher elevations it is on exposed places with shallow soil, strong insolation, or other factors favoring a xeric flora. The members of this sub-group display less tendency to avoid the Columbia and Deschutes areas. They have probably arrived at our lati-

tude by way of the system of valleys west of the Cascades or by way of the valleys and plateaus adjacent to the Great Basin east of this range.

Adenocaulon bicolor Hook.
Allium acuminatum Hook.
Amelanchier florida Lindl.
Apocynum pumilum (Gray) Greene
Asarum caudatum Lindl.
Bromus vulgaris (Hook.) Shear
Castilleja hispida Benth.
 var. *hispida*
Crocidium multicaule Hook.
Cryptantha hendersonii (Nels.) Piper
Delphinium menziesii DC.
Eriophyllum lanatum (Pursh) Forbes
Erysimum capitatum (Dougl.) Greene

Gilia capitata Hook.
Holodiscus discolor (Pursh) Maxim.
Koeleria cristata (L.) Pers.
Lilium columbianum Hans.
Lotus douglasii Greene
Madia gracilis (Smith) Keck
Microsteris gracilis (Dougl.) Greene
Pinus ponderosa Dougl.
Prunus demissa (Nutt.) Dietr.
Rhamnus purshiana DC.
Sedum douglasii Hook.
Trifolium microcephalum Pursh
Zygadenus venenosus Wats.

2. PUGET AREA ELEMENT. Another large group of species represented in the Gorge (54 in number and 26.2 per cent of the total) differs from the previously listed one in being restricted to the west side of the Cascade axis. They are, for the most part, common and widely distributed in the Puget Area and form a considerable part of its basic flora.

Acer circinatum Pursh
Acer macrophyllum Pursh
Achlys triphylla (Smith) DC.
Alnus oregona Nutt.
Anemone deltoidea Hook.
Arnica amplexicaulis Nutt.
Aruncus silvester Kostel.
 var. *acuminatus* (Dougl.) Jepson
Asplenium trichomanes L.
Brodiaea coronaria (Salisb.) Engler
Campanula scouleri Hook.
Cimicifuga elata Nutt.
Cornus nuttallii Aud.
Corydalis scouleri Hook.
Corylus californica (A. DC.) Rose
Delphinium oreganum How.
Dicentra formosa (Andr.) DC.
Dryopteris arguta (Kaulf.) Watt.
Fragaria bracteata Hel.
Gaultheria shallon Pursh
Hydrophyllum tenuipes Hel.
Iris tenax Dougl.
Mahonia aquifolium (Pursh) Nutt.
Mahonia nervosa (Pursh) Nutt.
Maianthemum bifolium DC.
 var. *kamtschaticum* (Gmel.) Jeps.
Melica harfordii Boland.
Montia parvifolia (Moc.) Greene
Oplopanax horridum (Sm.) Miq.
Oxalis oregana Nutt.
Oxalis trilliifolia Hook.

Penstemon ovatus Dougl.
Penstemon serrulatus Menz.
Phacelia nemoralis Greene
Philadelphus lewisii Pursh
 var. *gordonianus* (Lindl.) Jeps.
Plectritis congesta (Lindl.) DC.
Polypodium vulgare L.
 var. *occidentale* Hook.
Polystichum munitum (Kaulf.) Presl
Prunus emarginata (Dougl.) Walp.
 var. *mollis* (Dougl.) Brew.
Pyrola bracteata Hook.
Rhododendron macrophyllum D. Don.
Rhus diversiloba T. & G.
Ribes bracteosum Dougl.
Ribes sanguineum Pursh
Romanzoffia suksdorfii Greene
Rubus spectabilis Pursh
Sambucus callicarpa Greene
Stachys emersonii Piper
Struthiopteris spicant (L.) Weis.
Tellima grandiflora (Pursh) Dougl.
Tiarella trifoliata L.
Tolmiea menziesii (Pursh) T. & G.
Tsuga heterophylla (Raf.) Sarg.
Vaccinium parvifolium Smith
Valeriana sitchensis Bong.
 var. *scouleri* (Rydb.) Piper
Vancouveria hexandra (Hook.) Morr. & Dcne.

3. COLUMBIA AREA ELEMENT. These species (27 in number, 13.2 per cent of the total) are typical members of the plant associations found in the Columbia Area, at least in its western portion, i.e., near the upper end of the Gorge. Some of them range beyond the confines of the area, occurring at relatively low elevations and in situations ecologically similar to those in the Columbia Area. When these occur west of the Cascades it is normally in the Rogue River Valley and southward, but not in the Puget Area.

- | | |
|--|---|
| * <i>Anemone oregana</i> Gray | * <i>Lupinus leucopsis</i> Agardh |
| <i>Arnica cordifolia</i> Hook. | var. <i>bingensis</i> (Suks.) C. P. Sm. |
| <i>Bromus tectorum</i> L. | <i>Microseris nutans</i> (Geyer) Schultz-Bip. |
| <i>Castilleja hispida</i> Benth. | * <i>Penstemon barrettae</i> Gray |
| var. <i>acuta</i> Penn. | <i>Penstemon richardsonii</i> Dougl. |
| * <i>Crepis barbiger</i> Leib. | <i>Penstemon subserratus</i> Penn. |
| <i>Dicentra cucullaria</i> (L.) Bernh. | <i>Philadelphus lewisii</i> Pursh |
| var. <i>occidentalis</i> (Rydb.) Peck | var. <i>lewisii</i> |
| * <i>Dodecatheon poeticum</i> Hend. | <i>Phlox speciosa</i> Pursh |
| <i>Eriogonum sphaerocephalum</i> Benth. | <i>Poa ampla</i> Merr. |
| var. <i>tenu</i> (Small) Piper | <i>Prunus emarginata</i> (Dougl.) Walp. |
| <i>Hackelia diffusa</i> (Lehm.) Johnst. | var. <i>emarginata</i> |
| <i>Helianthus cusickii</i> Gray | <i>Senecio integerimus</i> Nutt. |
| * <i>Hydrophyllum capitatum</i> Dougl. | var. <i>exaltatus</i> (Nutt.) Cronq. |
| var. <i>thompsonii</i> (Peck) Const. | <i>Silene douglasii</i> Hook. |
| <i>Iliamna rivularis</i> (Dougl.) Greene | <i>Spiraea lucida</i> Dougl. |
| <i>Lewisia rediviva</i> Pursh | <i>Trifolium macrocephalum</i> (Pursh) Poir. |
| <i>Luina nardosmia</i> (Gray) Cronq. | |
| var. <i>glabrata</i> (Piper) Cronq. | |

The six species preceded by an asterisk are of especial interest in that they occupy a very restricted region. They have their centers of distribution near the east end of the Gorge and are strictly endemic to this part of the Columbia Area. In the Gorge they usually occur toward the east end and, as might be expected, in fairly dry situations. Since the *Lupinus* and *Penstemon* species referred to here do not actually occur west of Mosier, it is doubtful whether they should be considered in our discussion of the Gorge flora. I list them merely because they form part of a flora which does have a definite relationship to the Gorge.

4. ROGUE AREA ELEMENT. A significant element of the Columbia Gorge flora (17 species, or 8.3 per cent) is typically associated with the oak-madrone woodland of the Rogue Area of southwestern Oregon (op. cit.), its components having their centers of distribution either there or farther to the south. However, they occur again rather frequently in the Columbia Area, especially in that portion near the upper end of the Gorge. These species rarely occur otherwise east of the Cascades. In the Puget Area they commonly appear as components of some rather striking islands of xeric vegetation growing on exposed rocky points in the Douglas fir belt (Detling, 1953). Their peculiar distribution pattern suggests the probability that during a warm, dry period they migrated northward from the

Rogue into the Puget Area, then eastward through the Columbia Gorge into the Columbia Area. During a succeeding cooler and moister phase of the climatic cycle these species have been much restricted in their occurrence in the Puget Area, and probably in the Gorge and in the Columbia Area as well.

Balsamorhiza deltoidea Nutt.
 Collinsia grandiflora Dougl.
 Collinsia parviflora Dougl.
 Comandra umbellata (L.) Nutt.
 Dichelostemma pulchellum (Salisb.)
 Hel.
 Eriogonum compositum Dougl.
 var. pilicaule St. J. & War.
 Godetia amoena Lilja
 Godetia quadrivulnera (Dougl.) Spach

Leptotaenia dissecta Nutt.
 Lotus micranthus Benth.
 Lupinus bicolor Lindl.
 Lupinus laxiflorus Dougl.
 Phacelia linearis (Pursh) Holz.
 Quercus garryana Dougl.
 Senecio harfordii Greenm.
 Triteleia grandiflora Lindl.
 var. howellii (Wats.) Hoover
 Viburnum ellipticum Hook.

5. BOREAL ELEMENT. A group of 31 species (15.1 per cent of the total) occurs normally at fairly high elevations in the Cascades, but is of interest here because its members are found rather abundantly at or near the bottom of the Gorge. Typically Canadian or Hudsonian Zone species, they usually range above 4000 feet. Some of them occur only in the Cascades, while others are found also in the mountain ranges both to the west and to the east of the Cascade axis; however, with only two or three exceptions they do not descend to the valley and plateau levels on either side. In the Gorge these species are nearly always found below the 1600-foot level, i.e., they are limited largely to the steep bluffs and cool lateral canyons, mostly on the south side of the river. In each case they are isolated from the main body of the population by a broad band of forested and less precipitous terrain in which I have so far found no record of their occurrence.

**Acer glabrum* Torr.
 subsp. *douglasii* (Hook.) Wesml.
 **Alnus sinuata* (Regel) Rydb.
 **Antennaria racemosa* Hook.
Arabis furcata Wats.
Arctostaphylos uva-ursi (L.) Spreng.
Arnica discoidea Benth.
 var. *eradiata* (Gray) Cronq.
 **Campanula petiolata* DC.
Cornus canadensis L.
Cryptogramma acrostichoides R. Br.
Dodecatheon dentatum Hook.
Dryopteris linnaeana C. Chr.
Habenaria unalaschensis (Spreng.)
 Wats.
Haplopappus hallii Gray
Lewisia columbiana (How.) Robins.
 **Lomatium angustatum* (C. & R.)
 St. John

Menziesia ferruginea Hook.
 var. *glabella* (Gray) Peck
Mitella trifida Graham
Penstemon nemorosus (Dougl.) Trautv.
Penstemon rupicola (Piper) How.
 **Phlox diffusa* Benth.
 subsp. *longistylis* Wherry
Polemonium carneum Gray
 **Polypodium vulgare* L.
 var. *columbianum* Gilb.
Populus tremuloides Michx.
 **Saxifraga bronchialis* L.
 var. *vespertina* (Small) Rosend.
 **Saxifraga caespitosa* L.
Saxifraga rufidula (Small) Macoun
 **Stenanthium occidentale* Gray
Suksdorfia violacea Gray
Trautvetteria grandis Nutt.
Vaccinium membranaceum Dougl.
Woodsia scopulina D. C. Eaton

Ten species of the foregoing list (designated by asterisks) constitute an interesting group because of their relationship to the flora of Saddle Mountain. This peak is located in Clatsop County, Oregon, about 75 miles northwest of the western portal of the Gorge. Although only slightly over 3200 feet in elevation, it is the site of an isolated boreal flora which it may be assumed was at one time continuous with that now found in the Olympic Mountains (Detling, 1954). At the present time this flora has been eliminated from the areas between Saddle Mountain and the Olympics, and occurs only occasionally southward in the Oregon Coast Range, e.g., on Marys Peak. The ten indicated Columbia Gorge species have this peculiar and interesting distribution, occurring also on Saddle Mountain and in the Olympics, but so far as we know not between these points.

6. ENDEMIC SPECIES. Of the 206 species considered here as representing the flora of the Columbia Gorge, seven are endemic to the Gorge:

Bolandra oregana Wats.
Douglasia laevigata Gray
var. *laevigata*
Erigeron howellii Gray

Erigeron oreganus Gray
Hieracium longiberbe How.
Sullivantia oregana Wats.
Synthyris stellata Penn.

It is true that two of those included in this category, *Bolandra oregana* and *Sullivantia oregana*, have been found at one other station outside the Gorge, namely at Elk Rock on the lower Willamette River, and thus are not truly endemic to the Gorge and in the strictest sense of the term; however, they must be considered here in any discussion of endemism as it relates to the history of the flora.

Elk Rock is a sheer cliff on the west bank of the Willamette River a few miles above Portland and twenty-two miles by air from the west portal of the Gorge at Crown Point. The face of the bluff has an easterly and slightly northerly exposure; in certain spots seepage water keeps the surface wet most of the time. Apparently conditions here are sufficiently similar to those in certain niches of the Gorge to have encouraged the persistence of a few rare plant species which are otherwise found only in the cool, misty vicinity of the waterfalls of the Gorge. This situation suggests that during some period of glaciation in the Northwest the cold was intense enough to cause the extension of the boreal flora from the Cascades out over the valley floor at least as far as the Willamette River.

There are two possibilities always to be considered regarding the origin of narrowly endemic species. In the first place, they may be of relatively recent origin, having risen through mutation or hybridization from some pre-existing species in the area they now occupy. Theoretically, given time and proper environmental conditions, such a species would be expected to increase in number of individuals and to extend into nearby territory. On the other hand, endemic populations may be relicts of species which once were more widely distributed, but which, due to some factor such as failure to cope with a changing environment have been reduced to their present limited range.

Viewed as a whole, the endemic species of the Gorge would seem to be of the latter type. This conclusion is based upon the occurrence of two of them isolated at Elk Rock, upon the fact that they seem to be morphologically stable and not undergoing further evolutionary development, and finally that for the most part they have no near relatives in the vicinity.

These seven species are well-defined entities, and the plant taxonomist has no difficulty in placing them in the category of "endemics." However, when one studies carefully the wide-ranging species represented in the Columbia Gorge his attention is soon called to the fact that evolutionary processes have frequently taken place in the Gorge, and presumably are still going on, which have made that portion of the species slightly, but still noticeably, different morphologically from the rest of the population. Specialists in certain groups have already called attention to some of these, e.g., Cronquist (1955) for *Arnica amplexicaulis* and *Haplopappus hallii*, but they are frequently loath to give such local forms taxonomic standing. However, we cannot ignore the fact that they are there, and if we wished to follow the lead of less conservative botanists and give varietal or subspecific names to these local entities we could increase considerably the number of endemics in our list. These would of course be of the first type as to origin.

GENERAL DISCUSSION

Viewed from the standpoint of the major migrations of the Pacific Northwest flora, there are two outstanding phases in which the geographical situation, physiographic features, and structure of the vegetation of the Columbia River Gorge are probably significant.

The first of these is the rôle of the Gorge as a gateway for the passage of lowland species from one side of the Cascade axis to the other. For the rather large number of species (81, or 39.4 per cent) now confined to one side or the other of the axis, the Gorge obviously has not fulfilled this function. Even among the 70 species with a general distribution both east and west it is unlikely that many have migrated through the Gorge. Judging from their present widespread occurrence they probably reached the vicinity of the Gorge by paralleling the range on either side.

There is evidence, however, that a significant number of lowland species from other groups listed above have migrated through the Gorge in assuming their present distribution. Chief among these are the Rogue Area species found in the Columbia Area, with their isolated occurrences in xeric islands west of the Cascades. It was inferred in the earlier brief discussion of this group that the migration of its members through the Columbia Gorge took place from west to east. The basis for this inference is the fact that the centers of distribution of these species are to the south and west today, and any evidence of former occurrence is now found west of the Cascades. *Quercus garryana* may be cited as an example. This migration probably took place at a time of maximum northward extension of the Rogue flora. Floral migrations from an areal center normally occur

while climatic conditions at the center are becoming intensified and the environment in advance of the migration is becoming progressively more like that of the center. Since essentially the Rogue Area center is relatively warm and dry, the northward extension of the Rogue flora probably coincided with a xerothermic phase in the climatic cycle of the Pacific Northwest. Studies on post-glacial forest succession in the Northwest, based upon pollen profiles from peat bogs (Hansen, 1955), indicate that such a warm, dry phase did set in approximately 8000 years ago and lasted until about 4000 year ago, with its maximum probably about 6500 years from the present.

The other distinctive feature of the Gorge flora is the fact that such a large part of it constitutes an island of boreal forms isolated at the bottom of the main canyon or its smaller tributary canyons. These are in all probability relict occurrences, left from a time when the boreal flora, pushed to lower levels from above, was continuous from the middle mountain elevations down to the present valley level. It is hard to conceive that such a large number of species would have been established at their present levels by being transported from higher elevations across a transitional zone during a period of temperate climate. Rather, it is more likely that there was a general downward shifting of the flora during a cold phase of the climatic cycle, and subsequent isolation of many of the species in favorable niches as the climate became warmer and the main populations of the boreal species retreated to higher elevations. The presence of a number of Columbia Gorge species on Saddle Mountain and in the Olympics is another indication of a former continuity of the boreal flora at low levels in this part of the Pacific Northwest.

The narrow endemics briefly discussed above were probably reduced to their present restricted range during or following the culmination of this cold maximum. The occurrence of some of these isolated along the lower Willamette River may indicate that at one period their range at valley level was considerably more extensive.

The cold maximum which caused the downward migration of the boreal species must have preceded the warm, dry phase of climate previously mentioned, as the pollen profiles indicate only moderate cooling in the last 6000 years. These same profiles, correlated with radiocarbon datings (Broecker, Kulp, and Tucek, 1956), indicate that the last major cold maximum in this part of the continent occurred about 12,000 years ago, a time probably coinciding with the maximum advance of the last continental ice sheet in western North America.

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THE GENUS *COLLINSIA*. III. THE SIGNIFICANCE OF CHIASMATA FREQUENCIES AS A CYTOTAXONOMIC TOOL¹

E. D. GARBER

The genus *Collinsia* Nutt. (Scrophulariaceae) includes twenty-one recognized species, divided into two groups (Newsom, 1929; Pennell, 1951). The species in one group have "sessile" flowers congested in whorls, with pedicels shorter than to no longer than the calyces of the lower whorls, and with flat, mature seeds. The species in the other group have pedicelled flowers, either solitary or in whorls, with the pedicels of the flowers of the lower whorls from as long as to longer than the calyces, and with either flat or thick, mature seeds. There are other differences between the species in these two groups but they are not as clear as those which have been mentioned. The basic chromosome number for the genus is 7; no polyploid species have yet been found (Garber, 1956, and unpubl.).

The species in each of the two groups apparently differ in their mean number of chiasmata per bivalent at metaphase I. With the exception of *C. corymbosa* Herder, the species with "sessile" flowers have mean values of 1.1-1.5 and the species with pedicelled flowers, 1.7-1.9 (Garber, 1956). *Collinsia corymbosa* was placed in the species group with "sessile" flowers by both Newsom (1929) and Pennell (1951), yet its combination of characters shows it to be somewhat intermediate between these two groups of species (Garber and Gorsic, 1956). The flowers are borne in dense, capitate whorls on pedicels 3-7 mm. long, with calyx lobes approximately 5 mm. long, and the mature seeds are thick. The mean number of chiasmata per bivalent at metaphase I in *C. corymbosa*, however, has been found to be 1.7-1.8, a value characteristic of the group of species with pedicelled flowers.

This paper presents evidence regarding the validity of chiasma frequency as a cytotonomic tool in studying relationships among species of *Collinsia* by considering the chromosome associations and aberrations

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in interspecific hybrids involving *C. heterophylla*, a species with "sessile" flowers.

TABLE 1. A comparison of certain morphological characters of *C. corymbosa*, *C. heterophylla*, and their interspecific hybrids (hcy 56632).

Character	Character <i>C. heterophylla</i>	Interspecific hybrid	<i>C. corymbosa</i>
Flower, position	"sessile"	<i>corymbosa</i> -like	"sessile"
Flower, upper lobes, length	prominent	intermediate	rudimentary
Flower, upper lobes, markings	present	present	absent
Flower, lateral lobes, color	blue-red	segregating*	cream white
Flower, tube color	pale blue-red	light blue	light blue
Flower, upper stamen filaments	basal spurs	no basal spurs	no basal spurs
Calyx lobes	glabrous	hairy, glandular	hairy, glandular
Leaf petiole	short	long	long

* Pale or light blue.

MATERIALS AND METHODS

For the current studies, plants were grown from seed which was kindly supplied by Dr. R. Bacigalupi. Of the species involved, *C. corymbosa* is apparently restricted to the area around Fort Bragg, Mendocino County, California; *C. heterophylla* Buist, typical of the group with "sessile" flowers, may be found throughout the hilly portions of the western regions of California from the extreme south almost to the Oregon boundary; *C. sparsiflora* Fisch. and Mey., representative of the pedicelled group, occurs at low and middle elevations northward in the California coast ranges from Marin County and in the Sierra Nevada from Tuolumne County to Butte County.

Clusters of buds were fixed in a solution (6:3:2) of methanol, chloroform, and propionic acid (Pienaar, 1955), which proved superior to the familiar alcohol-acetic acid fixative, and the buds were then stored in a deep freezer until needed. Smears of pollen mother cells were stained with acetocarmine. Pollen grains were stained with basic fuchsin in lactophenol.

HYBRIDIZATION RESULTS

Interspecific hybridizations involving "sessile"-flowered *C. heterophylla* and *C. corymbosa* were easily accomplished. The yield and quality of the resulting seeds were excellent and approximately 90 per cent of the seeds germinated. Interspecific hybridizations involving the pedicelled-flowered species *C. sparsiflora* and *C. corymbosa*, however, were almost completely unsuccessful.

TABLE 2. Chromosome configurations at metaphase I in interspecific hybrids (hcy 56632) between *C. corymbosa* and *C. heterophylla*.

II	I	III	IV	Plant No.			
				3	5	6	10
7	----	----	----	14	48	42	19
6	2	----	----	19	15	61	18
5	4	----	----	12	4	24	18
4	6	----	----	2	----	4	4
3	8	----	----	----	----	2	----
5	1	1	----	1	2	----	1
4	3	1	----	----	----	1	----
3	5	1	----	1	----	1	----
5	----	----	1 chain	----	1	2	1
5	----	----	1 ring	----	----	----	1
4	2	----	1 chain	----	----	1	2
4	2	----	1 ring	----	1	----	1
3	4	----	1 chain	----	1	----	1
No. of pollen mother cells				49	72	138	66

MORPHOLOGICAL STUDIES. Only the interspecific hybrids between *C. heterophylla* and *C. corymbosa* were studied. The morphological differences between these species are so obvious that there is no difficulty in distinguishing these species. Certain characteristics of each species and their hybrids are summarized in Table 1.

In general, the interspecific hybrids resembled *C. corymbosa* in their vegetative characteristics, but the flowers were more like those of *C. heterophylla*. The hybrids were intermediate in height but almost as tall as *C. heterophylla*.

CYTOLOGY. The chromosome associations at metaphase I in the interspecific hybrids are summarized in Table 2. Most pollen mother cells had univalents and bivalents. A few pollen mother cells also had a trivalent or a quadrivalent. The mean number of chiasmata per bivalent at metaphase I in pollen mother cells with only bivalents was 1.3–1.4, which were the values observed for hybrids between *C. heterophylla* and *C. sparsiflora* (Garber and Gorsic, 1956).

No pollen mother cells had two trivalents or two quadrivalents. Since many pollen mother cells had univalents, it was conceivable that a ring of six chromosomes, the result of two reciprocal translocations involving one chromosome, could have been formed. Several configurations make this interpretation unlikely. The conclusion that at least a single heterozygous reciprocal translocation occurred in the interspecific hybrid appears to be reasonable. Pollen mother cells at telophase I often displayed a dicentric chromatid bridge and a very small fragment; a few cells had two bridges and two very small fragments (Table 3). These observations indicate that the interspecific hybrids had two heterozygous paracentric inversions.

TABLE 3. Number of pollen mother cells with dicentric chromatid bridges and fragments at telophase I in interspecific hybrids between *C. corymbosa* and *C. heterophylla*.

Plant No.	No. of bridges + fragments			No. of pollen mother cells
	0	1	2	
5	55	24	4	83
6	50	27	2	79
10	73	31	7	111

STERILITY. The interspecific hybrids were almost completely pollen-sterile, with less than 0.3 per cent stainable pollen grains. No seeds were set even when the flowers were hand-pollinated.

DISCUSSION

The group with "sessile" flowers includes the following species: *C. heterophylla*, *C. concolor*, *C. tinctoria*, *C. bartsiaefolia*, *C. multicolor*, *C. austromontana*, and *C. corymbosa* (Pennell, 1951). It has been possible to assemble data on the crossability, the fertility, and chromosome associations in interspecific hybrids involving *C. heterophylla*, *C. concolor*, *C. tinctoria*, and *C. bartsiaefolia* as well as in interspecific hybrids between *C. sparsiflora* and both *C. heterophylla* and *C. concolor* (Garber, unpub.; Garber and Gorsic, 1956; Hiorth, 1933).

When hybrids can be made between species, intragroup hybrids are more difficult to accomplish than intergroup hybrids, the yield of germinating seeds being much greater for the intergroup hybrids. Intragroup hybrids involving species with "sessile" flowers were fertile to some degree; intergroup hybrids were completely sterile. The hybrids between *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

Intragroup hybrids involving species with "sessile" flowers displayed only bivalents at metaphase I; intergroup hybrids had such chromosomal aberrations as heterozygous reciprocal translocations and heterozygous paracentric inversions. These chromosomal aberrations were responsible for the complete sterility of the intergroup hybrids. In this respect also, the hybrids involving *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

It seems reasonable to assume that barriers to hybridization have occurred for the species within the group with "sessile" flowers. Since such hybrids are fertile to some degree, such barriers would minimize the possibility of large scale introgression. The complete sterility of hybrids between species of different groups which easily hybridize serves as an effective barrier against introgression.

It is not yet clear what significance may be attached to the observation that hybrids between *C. corymbosa* and *C. heterophylla* have a mean number of chiasmata per bivalent at metaphase I of 1.3-1.4, a value also found in the interspecific hybrids involving *C. sparsiflora* and both *C.*

heterophylla and *C. concolor*. It is possible that this observation may be related to the length of the homologous segments in the chromosomes of the species in different groups.

Although the evidence may be interpreted to indicate that *C. corymbosa* does not belong with the species having "sessile" flowers, it appears more reasonable at this time to consider that *C. corymbosa* does not belong to the group of species including *C. heterophylla*, *C. concolor*, *C. tinctoria*, and *C. bartsiaefolia*. The other two species with "sessile" flowers, *C. multicolor* and *C. austromontana*, may yield critical information on this point. At any rate, the differences in the mean number of chiasmata per bivalent at metaphase I appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*. It must remain for future investigation to determine the extent to which this tool may be used.

SUMMARY

Interspecific hybridizations between *C. corymbosa* and *C. heterophylla* were easily accomplished, yielding a very high percentage of germinating seeds. The hybrids were completely sterile. Different numbers of bivalents and univalents were observed at metaphase I and, occasionally, a trivalent or quadrivalent was seen at the same stage. The multivalent was interpreted as a heterozygous reciprocal translocation. One or two dicentric chromatid bridges plus one or two very small fragments were observed at telophase I, indicating the presence of at least two heterozygous paracentric inversions. The combined data indicated that *C. corymbosa* does not belong with a number of species with "sessile" flowers but did not conclusively demonstrate that this species does not belong within the group of species having "sessile" flowers. The results indicate that differences in chiasma frequency appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*.

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